INTER- AND WITHIN-TROOP COMPETITION OF FEMALE RING-TAILED LEMURS: A PRELIMINARY REPORT

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ABSTRACT In a female-bonded/matrilineal group of primates, females may suffer from competition in both within- and inter-troop contexts. The balance between these two forms of competition was analyzed from the behavioral and demographic data recorded for a wild population of ring-tailed lemurs at Berenty Reserve, Madagascar. Within a troop, harsh and persistent aggressive behavior (targeting behavior) among female members ultimately evicted some victims. Troop size may influence the correlations between female rank and their reproductive parameters. In large troops, lower ranked females tended to show lower reproductive success than other females, but the differences were not significant. Birth rate and reproductive success (number of surviving infants) exhibited a humped curve against troop size, corresponding to Wrangham's IGFC (inter-group feeding competition) hypothesis. A troop may show the following cycle: First, a troop gains advantages via inter-troop competition, and increases in size. When optimal troop size is exceeded, the reproductive success of each female may decrease due to serious within-troop competition. Then, dominant females may evict subordinate females from the troop. The evicted females may form a new troop (troop fission), and transfer into other troops (i.e., female transfer/fusion), or die (group extinction).

Key Words: *Lemur catta*; Female competition; Rank; Reproduction; Ranging behavior.

INTRODUCTION

Since Darwin wrote "The Origin of Species" (1859), "female competition" has tended to be neglected from the discussion of animal societies (Small, 1989). On the other hand, many species of primates form a matrilineal/female-bonded social structure, in which the females of a group compete with one another for local resources (within-group competition), while at the same time they are forced to form coalitions against neighboring groups (inter-group competition) (Cheney, 1987).

There have been several hypotheses regarding such female competition in primates. It is still uncertain whether high-ranked females attain high reproductive success (RS) or not (Fedigan, 1983). Some authors report a significant correlation between female rank and RS (e.g., *Macaca mulatta*: Drickamer, 1974), but others do not (*Cercopithecus aethiops*: Cheney *et al.*, 1988). There are also diverse results concerning the correlation between RS and group size. Wrangham (1980) stressed the balance between within- and inter-group competition, and proposed a model in which birth rate (BR) should show a humped curve pattern against group size in his inter-group feeding competition (IGFC) hypothesis. In contrast, van Schaik (1983) emphasized the importance of predation pressure, and he proposed the predation-intra-group feeding competition (PFC) hypothesis in which BR and offspring mortality decrease linearly with group size. There are data to support both the PFC hypothesis (e.g., *Macaca silenus,* Kumar, 1995) and the IGFC hypothesis (e.g., *M. fuscata,* Takahata *et al.*, 1998). On the other hand, Sibley (1983) predicted that optimal group size may rarely be achieved, because groups will remain sub-optimally large rather than fission (Jolly *et al.*, 2002).

The ring-tailed lemur (*Lemur catta*) is a good species to investigate such questions (Jolly *et al.*, 2002; Koyama *et al.*, 2002). This species is a matrilineal/female-bonded prosimian (Jolly, 1972; Koyama, 1991). Troop size is small, and severe troop encounters frequently occur (Mertl-Millhollen *et al.*, 1979; Nakamichi & Koyama, 1997). Troop members, in particular adult females, compete for rank with one another, and persistent aggressive behavior (targeting behavior; Pereira, 1993) often occurs among them. Based on the demographic data recorded at the Berenty Reserve, southern Madagascar, Jolly *et al.* (2002) reported that BR fell in larger troops, corresponding to the PFC hypothesis, but that survival to one year after birth had no relation to troop size. They concluded that the effect of troop size on demography was closer to Sibley's (1983) model.

In this report, we analyze social relationships, ranging behavior, and reproductive data of a population of ring-tailed lemurs at Berenty, to measure the balance between within and inter-troop competition in a female-bonded/matrilineal society.

SUBJECTS AND METHODS

This study was carried out at the Berenty Reserve, southern Madagascar. For details on history and habitat, please see Jolly (1972), Koyama (1991), Oda (1996), and Koyama *et al.* (2001). The study population of ring-tailed lemurs has been individually identified by NK and his colleagues since 1989. In September 1998, the population included 100 individuals consisting of 6 multi-male and multi-female troops, and one female group (Koyama *et al.*, 2002).

From August 15th to October 4th 1997, YT observed four adult/subadult females and three adult males of Troop CX by the focal-animal sampling method (Altmann, 1974) for about 151 hours in total (Table 1). This troop had split away from Troop C1 in 1993 (Koyama *et al.*, 2002), and it contained 10 members including three adult females (>3 years), one subadult female (3-year-old), and three adult males (>3 years) in August 1997. Of the three males, KI-92 ♂ was born in Troop C2 and had transferred into Troop CX in 1995. The other two males (HAS and KUR) were born in unknown troops, and had transferred into Troop CX around 1995 and 1994 respectively. There was no systematic provisioning of this troop, but guides or tourists sometimes gave them food, e.g.,

Table 1. Observation minutes in each study period.

Period	Time	Activity: Troop encounter	Feed	Move	Rest/non-active	Total	
Period 1	-8:30	1	14	37	3	55	
	8:30	0	29	10	38	77	
	9:00	0	12	7	57	76	
	9:30	0	17	19	102	138	
	10:00	0	11	6	136	153	
	10:30	9	0	1	103	113	
	11:00	3	6	23	113	145	
	11:30	1	0	41	94	136	
	12:00	0	8	17	104	129	
	12:30	0	8	10	125	143	
	13:00	0	0	12	77	89	
	13:30	5	6	31	67	109	
	14:00	10	11	16	50	87	
	14:30	3	0	5	76	84	
	15:00	8	24	5	71	108	
	15:30	0	10	5	131	146	
	16:00	0	13	31	66	110	
	16:30-	0	6	12	27	45	
	Subtotal	40	175	288	1440	1943	32.83 hr
Period 2	-7:30	0	12	8	73	93	
	7:30	5	23	2	116	146	
	8:00	10	29	16	141	196	
	8:30	18	8	24	148	198	
	9:00	6	9	15	135	165	
	9:30	7	27	21	77	132	
	10:00	3	43	40	157	243	
	10:30	4	47	23	134	208	
	11:00	7	36	14	178	235	
	11:30	0	11	16	232	259	
	12:00	0	31	25	164	220	
	12:30	1	26	15	165	207	
	13:00	0	14	1	182	197	
	13:30	0	5	2	152	159	
	14:00	12	1	0	149	162	
	14:30	13	3	16	145	177	
	15:00	0	7	15	79	101	
	15:30	4	5	33	64	106	
	16:00	6	7	17	86	116	
	16:30-	3	6	2	39	50	
	Subtotal	99	350	305	2616	3370	56.17 hr

Period 3	-7:30	0	22	19	72	113	
	7:30	2	27	29	126	184	
	8:00	2	31	47	132	212	
	8:30	23	18	27	200	268	
	9:00	18	20	33	146	217	
	9:30	9	22	27	125	183	
	10:00	13	11	33	175	242	
	10:30	5	16	14	148	194	
	11:00	9	14	9	159	191	
	11:30	0	2	7	193	202	
	12:00	0	31	9	180	220	
	12:30	4	18	2	178	202	
	13:00	2	14	4	154	174	
	13:30	0	18	4	195	217	
	14:00	10	18	1	181	210	
	14:30	7	26	18	169	220	
	15:00	3	13	18	167	201	
	15:30	0	14	32	127	173	
	16:00	1	12	16	94	123	
	16:30-	2	8	19	40	69	
	Subtotal	110	355	368	2961	3815	63.58 hr

banana. In the center of Troop CX's range, there was an artificial water cistern, which they greatly depended on. YT recorded the ranging area of a neighboring troop, Troop C1 by focal-group sampling, and also recorded the ranging areas of two other troops (Troop A2 and D2) by ad lib sampling. To measure the area of their ranges, a 25m grid (0.0625 ha) was superimposed on the field maps (see Fig. 1).

Lemur activity was roughly grouped into four types: (1) feeding (including drinking), (2) moving, (3) resting/nonactive (including sunning, grooming, and playing), and (4) troop encounter. In Berenty, troops of ring-tailed lemurs frequently encountered with one another, and the encounters often lasted for several or more minutes. Mean duration of a troop encounter was 8.0 minutes (SD=11.3 minutes, n=53, range 0-48 minutes). For example, on 17 August, Troop CX encountered Troop C1 at 14:31. Two troops confronted each other until 15:09 when Troop CX withdrew.

Between 1996 and 1998, the demographic and dominance rank data of 18 troop-years were recorded by YT, NK, SI, and NM for Troop CX, C1, C2/C2A, C2B, T1, T2 and HSK group (for the history of each troop, see Koyama *et al.*, 2002). For each troop, we calculated the mean non-infant troop size, mean number of adult/subadult females (>2 yrs), birth rate (BR), and infant survival rate within one year after birth (ISR).

Dominance ranks among all adult members were determined according to the following interactions: (1) approach-retreat interactions while feeding and drink-

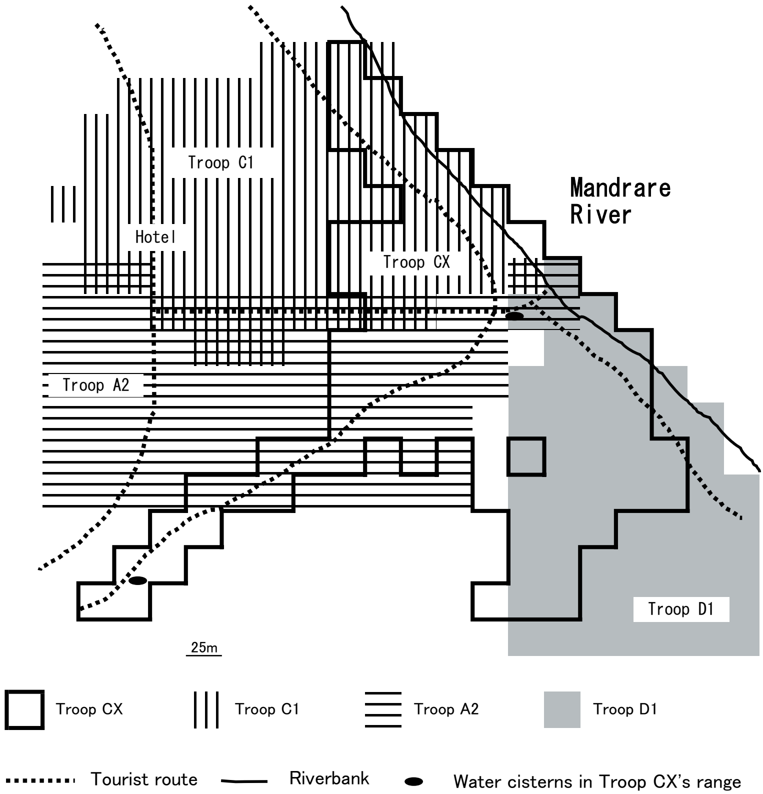

Fig. 1. Ranging areas of Troop CX and Troop C1, A2, and D1 during Periods 1-3.

ing, and (2) submissive vocalizations (spat calls). The individual who spat-called to another was considered the subordinate (Nakamichi & Koyama, 1997). Relative ranks of each female were also calculated for each study year and were adjusted according to the proportion of females over whom the female was dominant in each female hierarchy (i.e., the relative rank of an alpha female was 100%, and that of the lowest-ranked female was 0%). In each troop, females were grouped into high-ranking (>66.67%), middle-ranking (66.67-33.33%), and low-ranking (33.33%>).

Statistical analyses were done using Excel 2002 (Microsoft, 2001), Statistica (StatSoft Inc., 1999), and SPSS (SPSS Inc., 2000).

RESULTS

I. Within-and Inter-troop Competition of Troop CX in 1997

Table 2. Agonistic interaction observed among adult members of Troop CX during Period 1.

	CW-90 ♀	CW-9094 ♀	SH-92 ♀	MW-911 ♀	HAS	KUR	KI-92 ♂
CW-90 ♀	-	1	3	2			1
CW-9094 ♀		-	2	2	2		
SH-92 ♀			-	2			
MW-911 ♀				-	4		1
HAS					-	1	
KUR						-	1
KI-92 ♂							-

1. Dominance Rank Order of Troop CX in August 1997

In August 1997, there was a linear rank order among four adult/subadult females and three adult males (Table 2). As pointed out by preceding studies (e.g., Jolly, 1984), every adult female was dominant over all adult males.

Many studies have reported that alliances infrequently occur among ring-tailed females, and daughters do not always inherit their mother's rank (Pereira, 1993, Nakamichi & Koyama, 1997, Nakamichi *et al.*, 1997). But our data suggest that lemurs may show some tendencies of "dependent rank" or "rank inheritance" through female kin relations, just as reported for the female-bonded/matrilineal troops of Old World monkeys. In August 1997, one young female (CW-9094 ♀) was second-ranking, just below the alpha-rank of her mother (CW-90 ♀; see Table 2). Although CW-90 ♀ disappeared in 1998, CW-9094 ♀ succeeded to her mother's alpha-rank, and maintained it even in 2001 (T. Soma, unpublished data). In another case, as stated later, the third-ranking SH-92 ♀ was attacked and outranked by the fourth-ranking MW-911 ♀ in September 1997. Then, MW-911 ♀'s daughter (MW-91195 ♀) became dominant over SH-92 ♀. MW-91195 ♀ also maintained dominance over SH-92 ♀, even after MW-911 ♀'s death in August 1998 (Y. Takahata, unpublished data).

Among adult males, HAS occupied the fifth-rank, KUR the sixth-rank and KI-92 ♂ the seventh-rank in August 1997. However, as stated later, KI-92 ♂ began to dominate over two older males, and had outranked them by September (Y. Takahata & N. Koyama, unpublished data).

2. Inter-Troop Competition: Ranging Behavior and Troop Encounters of Troop CX

Throughout Period 1-3, Troop CX ranged in an area of 93 grids (5.8 ha). As shown in Fig. 1, most of their ranging area largely overlapped with those of the neighboring Troop C1, A2, and D1. Thus, their home range is not a classical "territory" defined for small birds by Howard (1920). Neighboring troops frequently invaded the center of Troop CX's range, because there was an artificial water cistern and several large tamarind trees (*Tamarinduous indica*) bearing many fruits, major food item for ring-tailed lemurs.

During the study period, three infants were born in Troop CX. Because parturition largely affected their ranging pattern and social relationships, the study period was divided into three stages; Period 1 (15-26 August), a period of no births; Period 2 (27 August - 12 September), a period of one birth; and Period 3 (13 September - 4 October), a period when the other two adult females gave birth.

Period 1 (15-26 August):

In this period, no female had given birth. Troop CX ranged in an area of 3.9 ha (Fig. 2a). Feeding occupied 9.0% of observation hours, moving 14.8%, resting/nonactive 74.1%, and troop encounter 2.1%. Troop encounters usually occurred around 9:00-10:00 and 14:00-14:30 (Fig. 3a). Feeding exhibited two peaks, morning and evening. Moving exhibited four peaks, early morning, around noon, around 14:00, and evening.

Troop CX frequently encountered Troop A2, C1, and D1. While in the center of their own range, Troop CX was dominant to even larger troops (Troop C1 had 20 members, and Troop A2 and D1 probably had 20 or more members). Out of the 18 encounters recorded in Period 1, Troop CX drove other troops away seven times and was driven away nine times. In two cases, the encounters ended in a draw. Thus, Troop CX had a small defensible area of about 1.6 ha, but other troops often ranged into even this area (Fig. 2a).

Troop CX intruded into the ranges of the neighboring troops, so called "excursions" as pointed out by Mertl-Millhollen *et al.* (1979). For example, on 26 August, the cistern in Troop CX's range dried up, and the troop eventually raided another cistern about 250 m from their regular range. They could drink water from the cistern, and continued to invade. However, an unidentified troop

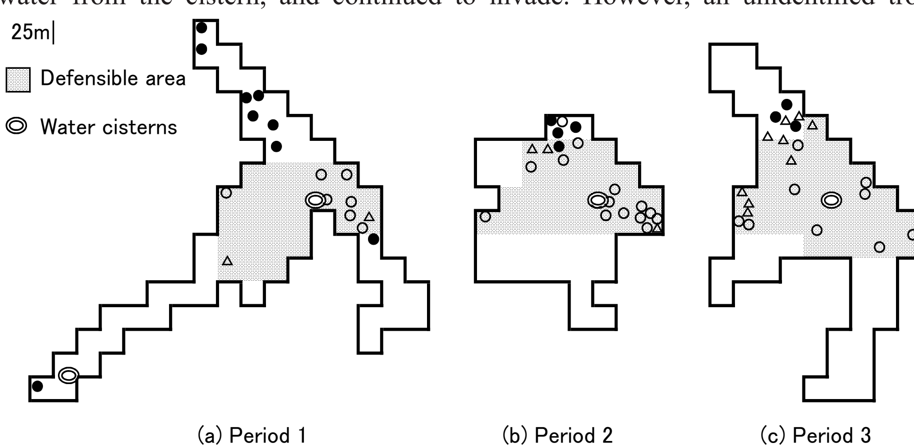

Fig. 2. Ranging areas of Troop CX in Period 1 (a), Period 2 (b), and Period 3 (c). ○: troop encounters in which Troop CX drove other troops away, Δ: troop encounters ending in a draw; ●: troop encounters in which Troop CX was driven away by other troops.

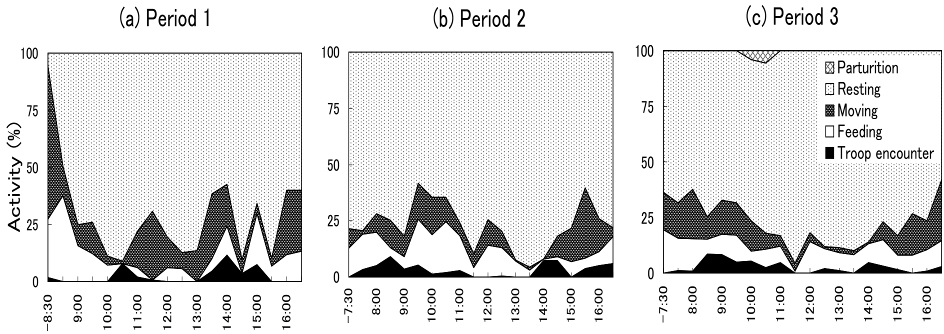

Fig. 3. Daily activity rhythm of Troop CX in Period 1 (a), Period 2 (b), and Period 3 (c).

appeared and charged them, and Troop CX rushed back to their own range.

Period 2 (27 August-12 September):

On 27 August, a low-ranking female, MW-911♀, gave birth, and other lemurs were strongly attracted to her newborn infant. MW-911♀ did not move widely, probably because of infant care. Consequently, the troop's ranging area decreased to 2.9 ha, and they rarely invaded other troop ranges (Fig. 2b). The third ranking male, KI-92♂, began to outrank other males, although direct aggressive interactions were scarcely observed.

Troop encounters were observed 22 times. Troop CX drove off other troops 15 times and were driven off 3 times. In 4 cases, the encounters ended in a draw. Apparently, the reduction of "excursions" resulted in the rise of the percentage of wins (39% of Period 1 → 68% of Period 2). The defensible area of the troop was about 1.5 ha.

Activity patterns also changed. The proportion of time spent moving to observation hours decreased from 14.8% in Period 1 to 9.1%. Feeding occupied 10.4% of the observation hours, resting/non-active 77.6%, and troop encounter 2.9% (see Fig. 3b). This proportion was significantly different from that of Period 1 (χ^2= 44.79, df=3, p<0.001).

Period 3 (13 September-4 October):

CW-90♀ gave birth on 12 September, and SH-92♀ gave birth on 13 September. Just after SH-92♀'s parturition, MW-911♀ attacked and outranked her. Throughout this period, MW-911♀ continued to harass SH-92♀. SH-92♀ usually grimaced to MW-911♀, and avoided her approaches. The ranging area increased to 3.8 ha in total (Fig. 2c). Troop encounters were observed 21 times. Troop CX drove off other troops 9 times and was driven off 3 times. In 9 cases, the encounters ended in a draw. The percentage of wins decreased to 43%, and the defensible area was about 1.9 ha.

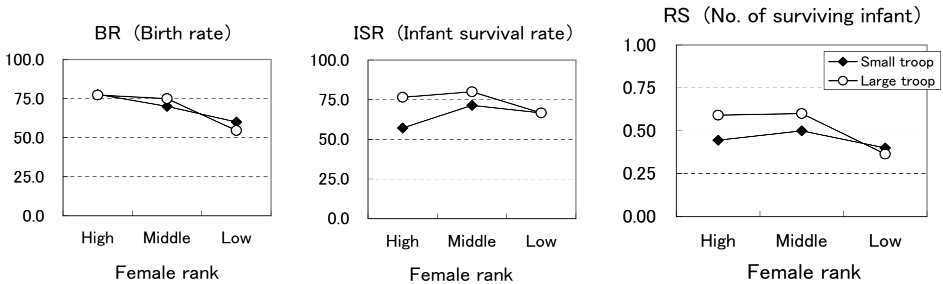

Fig. 4. Correlations between female rank and reproductive parameters (BR, ISR, and RS) in small troops and large troops.

Excluding the 21 minutes recorded for SH-92♀'s delivery, feeding occupied 9.4% of the observation hours, moving 9.7%, resting/non-active 78.0%, and troop encounter 2.9% (Fig. 3c). This proportion was not different from that of Period 2 (χ^2=2.77, df=3, p>0.3), but significantly different from that of Period 1 (χ^2=35.72, df=3, p<0.001).

II. Female Rank and Reproductice Success

Do higher-ranking females show higher reproductive success? Calculated from the birth data recorded for seven troops/groups (Troop CX, C1, C2/C2A, C2B, T1, T2 and HSK group) from 1996 to 1998, there was no significant difference in birth rate (BR), infant survival rate (ISR) and number of surviving infants within one year after birth (RS) among female rank groups (χ^2=3.15, df=2, p>0.2; χ^2= 0.572, df=2, p>0.7; χ^2=2.23, df=2, p>0.3).

Troop size may influence the correlations between female rank and their reproductive parameters. In small-sized troops with five or less adult females, there were no consistent difference in BR, ISR, and RS (χ^2=0.300, df=1, p>0.8; χ^2=0.324, df=1, p>0.8; χ^2=0.271, df=1, p>0.8) (Fig. 4). On the other hand, in large-sized troops with six or more adult females, low-ranking females exhibited lower BR, ISR, and RS values than other females, although the differences were not significant (χ^2=3.17, df=1, p>0.2; χ^2=0.664, df=1, p>0.7; χ^2=3.10, df=1, p>0.2).

III. Troop Size and Female Reproductive Success

Were the reproductive parameters of ring-tailed lemur females correlated with troop size? BR, ISR, and RS of Troop C1, C2A, C2B, CX, T1 and T2 did not show a linear correlation with troop size (Pearson's r=0.297, p>0.5; r=-0.037, p>0.9; r=0.206, p>0.6), nor with the number of adult females (r=0.11, p>0.9; r=0.063, p>0.9; r=0.055, p>0.9). BR and RS instead exhibited a rather humped curve against troop size (BR; r^2=0.632, F=2.58, p=0.223; ISR, r^2=0.083, F=0.14, p=0.879; RS, r^2=0.635, F=2.61, p=0.221) (Fig. 5a), and number of adult females (BR; r^2=0.547, F=1.81, p=0.305; ISR, r^2=0.020, F=0.03, p=0.970; RS, r^2=0.512,

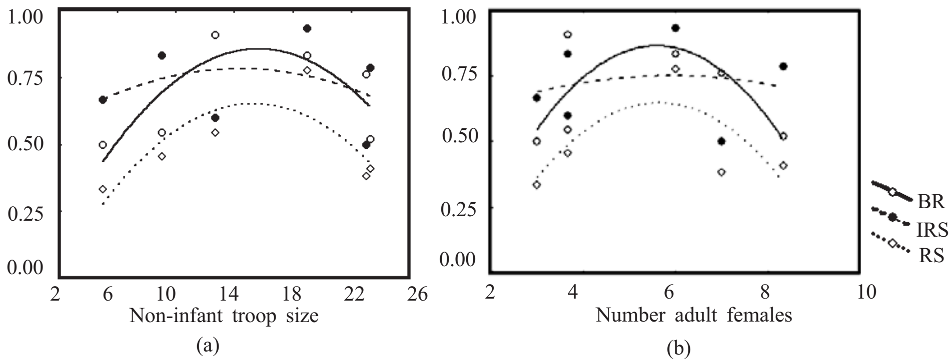

Fig. 5. Correlations between the reproductive parameters (BR, ISR, and RS) and troop size and number of adult females.

F=1.58, p=0.341) (Fig. 5b).

DISCUSSION

I. Ranging and Defenese Behvior of Ring-Tailed Lemurs

In a matrilineal/female-bonded society, females of a group should compete for local resources with one another (within-group competition), but they should be forced to form coalitions among themselves against neighboring groups (inter-group competition) (Wrangham, 1980; Cheney, 1987). At Berenty, Madagascar, ring-tailed lemurs show such a dual competition structure under some predation pressure, e.g., raptors. Each troop actively defends their range against neighboring troops (Jolly, 1972; Koyama, 1991; Nakamichi & Koyama, 1997), and they also invade the ranges of other troops in "excursions" described by Mertl-Millhollen *et al.* (1979). Within the troop, there is a linear dominance rank order, and the females compete for higher rank with one another through "targeting behavior" (Pereira, 1993).

During the present study, the ranges of neighboring troops largely overlapped with one another. Every troop actively and frequently invaded the ranges of neighboring troops. Whereas Troop CX had a small defensible area of about 1.5 -1.9 ha around the center of their range, other troops often ranged into even this area. Thus, the present state of their range is not a classical "territory" as has been reported for small birds (Howard, 1920), or gibbons (Tenanza, 1975).

On the other hand, Jolly (1972) reported that, in the 1960s, the overlap in troop ranges was slight at Berenty. Then, the overlapping and inter-troop aggression may have increased through the 1970s, which might have originated from the population increase (Mertl-Millhollen *et al.*, 1979). Jolly (1972) estimated a population density of 350 lemurs/km^2 in 1964. In the same area, Koyama *et al.* (2002) noted a gain to 440 lemurs/km^2 in 1989, and 580 lemurs/km^2 in 1998. Interestingly, a similar phenomenon was recorded by the long-term study of wild Yakushima macaques (*Macaca fuscata yakui*), a subspecies of Japanese macaques. In the 1970s, the population density was low (ca. 30 monkeys/km^2), and each troop had a defensible and territorial range. Then the density increased to about 80-100 monkeys/km^2 (Yoshihiro *et al.*, 1999), and the ranges of neighboring troops came to largely overlap one another. Troops aggressively encountered one another in such overlapping areas (Saito *et al.*, 1998). Thereafter, several cases of troop extinction and female transfer occurred (Sugiura *et al.*, 2002). Thus, the increase of population density may have affected the ranging and territorial behaviors for both populations of Yakushima macaques and ring-tailed lemurs.

II. The Balance Between Inter-Troop and Within-Troop Competition

There is no clear cut correlation between female rank and reproductive success in primates (Fedigan, 1983). Some reports indicate a positive correlation (e.g., *Papio cynocephalus,* Smuts & Nicolson, 1989; *Macaca fascicularis*, van Noordwijk, 1999), but others do not (*M. fuscata*, Wolfe, 1984). The present data were too small to make a conclusion for ring-tailed lemurs on this question. However, the data available suggest that, as van Noordwijk (1999) pointed out for long-tailed macaques, female RS might be affected by group size. In larger-sized troops, the lower-ranking females had a smaller number of surviving infants, although the differences were not significant. Note that in this species, female rank order frequently changes by severe and persistent aggression. The correlations between a particular female and her lifetime reproductive success should be recalculated based on long-term data.

There is another discrepancy in the discussion of the correlation of group size and female reproductive success in matrilineal/female-bonded societies, i.e., the two competing hypotheses of IGFC (Inter-group feeding competition) by Wrangham (1980) and PFC (Predation-intra-group feeding competition) by van Schaik (1983). For example, BR linearly decreased with troop size in a population of lion-tailed macaques, corresponding to the PFC hypothesis (Kumar, 1995). In contrast, the data on *Cebus olivaceus* corresponded to the IGFC hypothesis (Robinson, 1988). Takahata *et al.* (1998) reported that the birth data of wild populations of Japanese macaques also agreed with the IGFC hypothesis, but that these data do not refute the PFC hypothesis either, because there was no predation pressure on Japanese macaque populations. For ring-tailed lemurs, at Berenty, Jolly *et al.* (2002) found that birthrate fell in larger troops, corresponding to the PFC hypothesis, but mortality had no relation to troop size, and Jolly *et al.* concluded that the effect of troop size on demography was closer to Sibley's (1983) model, i.e., suboptimally large by any measure.

The present data is small, but it suggests that the BR and RS (number of surviving infants) of ring-tailed lemur females shows a humped curve against the non-infant troop size, supporting the IGFC hypothesis, and differed from the conclusion of Jolly *et al.* (2002). This may be because the density of our study population (654.9 individuals/km^2 in 1997) is much higher than the 280 individuals/km^2 of the study population of Jolly *et al.* (2002), i.e., the whole population of Berenty Reserve. Such a high density should have intensified inter-troop competition, and may have lowered the fecundity of small-sized troops in our study area.

Thus, ring-tailed lemur females may suffer from the dual competition structure of matrilineal/female-bonded society, as suggested by Wrangham (1980). During the 10-year period, eight troop fissions, six female evictions, and three troop takeovers of ranges occurred in and around our study population (Koyama *et al.*, 2002). Most troop fission/evictions of females occurred in large-sized troops consisting of 20 or more lemurs, and likely originated from female competition.

A ring-tailed lemur troop may show the following cycle. First, a larger-sized troop may gain advantages over other troops in inter-troop competition, and continue to increase in size. However, if troop size exceeds its optimal level, the reproductive success of each female may begin to decrease, due to within-troop competition. In such a situation, some females may leave the troop, or be compelled to do so by other females.

At Berenty, many females were compelled to leave due to targeting aggression from other females (Koyama *et al.*, 2002). If such females can establish new home ranges and gain mating partners elsewhere, a new troop may be formed. If the females cannot establish home ranges, they could be forced to transfer into another troop (female transfer or troop fusion), or might die (group extinction). Furthermore, many other costs and risks should be expected with leaving a troop, such as the acquisition of a new home range and mating partners and avoidance of predation. These factors might restrain females from voluntarily deserting a troop.

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